

Detecting the Geographical Pattern of Speciation from Species-Level Phylogenies

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ABSTRACT: We introduce a general approach for investigating the role of geography in speciation, based on analyzing the geography of sister clades across all nodes in a species-level phylogeny. We examine the predictions of allopatric, sympatric, and peripatric models of speciation in several animal groups, using patterns of range overlap and range size symmetry between sister clades. A simple model of cladogenesis incorporating random movements of species' ranges is used to illustrate the effects of range changes on expected patterns. We find evidence for a predominantly allopatric mode of speciation in our study groups, with sympatry arising through post-speciational range changes. In addition, we find that relatively recent speciation events are characterized by greater asymmetry in range size between sister clades than expected under our null models, providing potential support for the peripatric model of speciation. We discuss the possible confounding effects of postspeciational range changes on our conclusions.

Keywords: speciation, diversity, null models, biogeography, modes.

The molecular revolution in phylogenetics has provided new sources of information for the study of evolution and macroecology, answering questions that were difficult to address until recently (Lutzoni and Pagel 1997; Omland 1997; Bleiweiss 1998; Farrell 1998; Losos et al. 1998). One area gaining new vitality from this information is the study of speciation. Phylogenies represent the pattern of cladogenetic splits leading to present-day species and may provide a trace of processes involved in the origin of those

species (Nee et al. 1996; Purvis 1996; Sanderson and Donoghue 1996; Barraclough et al. 1998, 1999a). Hence, publication of large numbers of species-level phylogenies will provide the opportunity for a comparative biology of speciation across a range of groups. However, this approach involves reconstructing past events, and so it is important to consider how changes occurring since speciation events influence our ability to infer the pattern of speciation (Mayr 1963). In this article, we investigate one particular issue, namely the use of species-level phylogenies for investigating the role of geography in speciation.

Geography is widely recognized as the key factor in the study of speciation. The primary classification of speciation, into so-called geographic modes, is based on the pattern of geographic ranges seen among daughter species (Mayr 1963; Bush 1975; Templeton 1981). However, the theoretical and empirical basis for different modes remains controversial, with particular emphasis on two issues. First, there is the question of whether geographical isolation is necessary for the formation of new species, resulting in debate over the relative frequencies of allopatric and sympatric speciation (Mayr 1963; Maynard Smith 1966; Rosenzweig 1978; Bush 1994; Doebeli 1996; Duffy 1996; Johnson et al. 1996; Shoemaker and Ross 1996). If allopatric speciation is the predominant mode, then we need to explain the subsequent origin of sympatry within clades. Second, within the context of allopatric speciation, many authors advocate the importance of small, founder populations in the process of speciation (Mayr 1963; Carson and Templeton 1984). This view is manifest in the prediction of the peripatric theory of speciation that new species tend to form as small range fragments around a widely distributed ancestral species. An alternative view is that speciation is caused by geographic features that split a species' range and that these may arise at any point within the ancestral species' range. Active debate over these two alternatives persists to the present day (Barton and Charlesworth 1984; Rice and Hostert 1993; Coyne 1994; Moya et al. 1995; Slatkin 1996, 1997; Templeton 1996; Charlesworth 1997).

The original evidence for these discussions was based

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on analyses of species' ranges, in the light of systematic revisions of genera (reviewed in Mayr 1963). Recent authors have performed more strictly statistical tests using phylogenetic information on monophyletic groups of species. For example, Chesser and Zink (1994) assessed the relative frequencies of different modes of speciation among a sample of American bird groups, following criteria used by Lynch (1989). However, the authors recognized two problems with the approach. First, it relies on an arbitrary classification of modes of speciation, depending on threshold values in the proportion of overlap between sister species or their relative range sizes. Second, species' ranges may have changed subsequent to speciation, in which case the distribution of newly formed species at the time of the split may no longer be recognizable from current ranges. In addition, previous accounts have not compared observed patterns to those predicted by explicitly stated models of the geographic mode of speciation. For example, in relation to the peripatric mode of speciation, the observed frequency of peripheral species with small range sizes may not be unusual compared to that expected simply by splitting the ancestral range into two randomly sized fragments.

We propose an approach based on analysis of the geographic ranges of species within a clade in the light of their phylogeny. Species-level phylogenies reconstruct the pattern of cladogenesis leading to extant species, and so the geographic ranges of sister clades identified from the phylogeny can be used as an estimate of the geographic mode at the time of speciation. In addition, subsequent range changes may be accounted for in part by considering the pattern of geographic ranges for sister clades across all nodes in the phylogeny (Brown and Gibson 1983; Lynch 1989; Chesser and Zink 1994). Deeper nodes in the phylogeny represent relatively older speciation events; therefore, changes in pattern with relative node age may reflect the extent of changes in geographic ranges over time. Hence, our approach is to calculate measures of geographic mode of speciation, such as range overlap between sister clades, for all nodes in the phylogeny and to consider the pattern of those measures in relation to the relative age of nodes. We introduced this approach briefly elsewhere (Barraclough et al. 1998, 1999a) but develop it further in this article. To illustrate the effects of range movements, we introduce a simple simulation model of cladogenesis, incorporating random movements of species' ranges within a continuous area. We use our findings to interpret real examples from bird, fish, and insect groups and discuss the likely utility of this approach for distinguishing modes of speciation.

Material and Methods

We performed a literature search for molecular phylogenies including all, or a large majority of, described extant species within clades for which species' range data are available. The chosen groups are not an exhaustive list of all such clades but were chosen to illustrate the method. Details are given in the appendix. They cover a range of animal groups and molecular markers. In many cases, the authors present several phylogenies obtained using different methods of phylogenetic reconstruction. We chose parsimony trees for consistency: nearly all papers presented parsimony trees, whereas distance methods varied among studies. The one exception was the phylogeny of *Sylvia* warblers, which was reconstructed by the distance-based method of DNA-DNA hybridization. We used the Fitch-Margoliash tree presented for this group. The relative ages of nodes were calculated by applying a local molecular clock approach to distance data for the chosen topology. This involves progressively averaging branch lengths for sister taxa, starting from the tips through to the base, and then using distances to nodes as estimates of relative age. Phylograms of each group suggest at least rough rate constancy among lineages within these groups. The use of branch lengths to estimate relative ages of nodes will be discussed below.

Species' ranges were obtained from sources listed in the appendix. Ranges were redrawn from source material as shaded regions onto equal area maps in the computer. Some sources provide shaded regions of species occurrence, others provided dot maps of localities. We drew shaded regions around dot maps by eye, following text descriptions of the ranges of each species. Computational methods of representing species' ranges for these groups could be employed, but for present purposes, these would be unlikely to lead to major differences in final ranges and in our conclusions. The ranges of higher clades were obtained by shading the area where at least one constituent species is found.

Allopatry or Sympatry

Methods

Using the shaded range maps, we calculate the degree of sympatry between sister clades for each node in the phylogeny of each group. The degree of sympatry is defined as the percentage of the more restricted clade's range overlapped by its more widespread sister (Chesser and Zink 1994):

$$\frac{\text{area of overlap}}{\text{range size of clade with smaller range}}$$

This ranges from 0.0, signifying no range overlap, to 1.0, signifying that the range of one clade is entirely overlapped by its sister. The index differs from one we used previously where our aims included testing for character divergence between sympatric lineages (Barraclough et al. 1998, 1999a, 1999b). Areas and overlaps were calculated by image analysis of the range maps. As a measure of time since speciation, we use the relative distance of each node from the tips of the phylogeny, based on branch length data obtained from source phylogenies. This assumes that branch lengths provide at least rough information on the relative ages of each node. We have repeated our analyses using an alternative measure, node level, which is the level of each node above the tips of the phylogeny: sister species are level 1, their nesting clade is level 2, and so on. The results are statistically indistinguishable, and so for brevity we present only those using relative branch length data. Potential limitations of this measure are discussed below. We plot the degree of sympatry against relative node age.

Predictions and Simulations

Elsewhere, we made verbal predictions for the expected patterns of these plots under alternate scenarios (Barraclough et al. 1998, 1999a), which can be summarized as follows: If speciation is predominantly allopatric, recently diverged sister species are expected to display little or no overlap in geographic ranges. Alternatively, if speciation is predominantly sympatric, recently diverged sister species are expected to display sympatries of around 1.0 because one species' range must enclose the other entirely. Hence, the intercept of the plot between range overlap and node age provides a summary of the predominant geographic mode of speciation within a clade. The level of range overlap between more anciently diverged sister clades depends on the extent of range movements occurring after speciation events. If speciation is predominantly allopatric, newly formed species have nonoverlapping ranges, and so subsequent range changes are likely to increase overlap between more anciently split species (at least for clades occupying a finite area). No increase in the observed range overlap between sister clades at older nodes is expected if there are no range movements subsequent to speciation. Hence, if speciation is predominantly allopatric, the slope of the plot between range overlap and node age provides a summary of the extent or rate of postspeciation range movements. Range changes may include changes in range size and shape, as well as drifting of ranges across the landscape. If speciation is predominantly sympatric, then range overlap is likely to decrease for relatively older nodes.

The predictions can be illustrated using a simple simulation model for the origin and movements of species' ranges during cladogenesis, outlined in figure 1. The model

combines a standard stochastic, constant birth rate model of cladogenesis (Raup et al. 1973; Harvey et al. 1994), with species' ranges coded for simplicity as rectangular shapes within a continental area. At speciation, the ranges of descendent species are determined by the chosen mode of speciation, either allopatric or sympatric. Ranges are free to move by random independent changes to their edges, leading to changes in size, shape, and location of species' ranges over time. The exact form of range movements may influence expected patterns, so we consider two alternatives differing in the relative frequency and magnitude of changes. The first is that ranges move by frequent but small-scale changes to their boundaries, such that boundaries undergo a random walk over time. The second is that range movements occur by occasional large-scale shifts of entire species' ranges, such as those observed in many temperate groups during periods of climate change (Coope and Wilkins 1994; Graham et al. 1996). Details are shown in figure 1. We do not include extinction in our model but discuss its likely impact on observed patterns in the discussion. The model is not intended to cover all possible scenarios; it is merely the simplest model incorporating mode of speciation and random changes to two-dimensional species' ranges.

Sample plots obtained by simulation are shown in figures 2 and 3. Under an entirely allopatric model of speciation (figs. 2A, 3A), range movements lead to increased sympatry between more ancient sister clades, which is largely associated with an increase in variance. The same pattern is found whether range changes occur by gradual accumulation of small-scale changes to range boundaries (fig. 2) or by occasional large-scale shifts of species' ranges (fig. 3). A high frequency of sympatric speciation increases the number of recent splits with sympatries around 1.0, leading to an increase in intercept (figs. 2C, 3C). However, as the level of range movements increases, plots generated under alternate modes of speciation become harder to distinguish: intercepts converge on an intermediate value, as shown by repeated trials summarized in figure 4. Note that, because our measure of sympatry is bounded between 0.0 and 1.0, the degree of sympatry was arcsine transformed before fitting intercepts to the plots by linear regression (Sokal and Rohlf 1981).

The effects of range movements can be treated further by considering the expected pattern when geographic ranges have changed so much that present-day ranges retain no information on the geographic mode of speciation. Even if species' ranges are randomly distributed shapes within a continental area, range overlap is likely to be greater between sister clades originating from older nodes. Older clades tend to occupy a larger area than younger clades because they contain more species, and thus, there is greater chance of range overlap with their sister clades

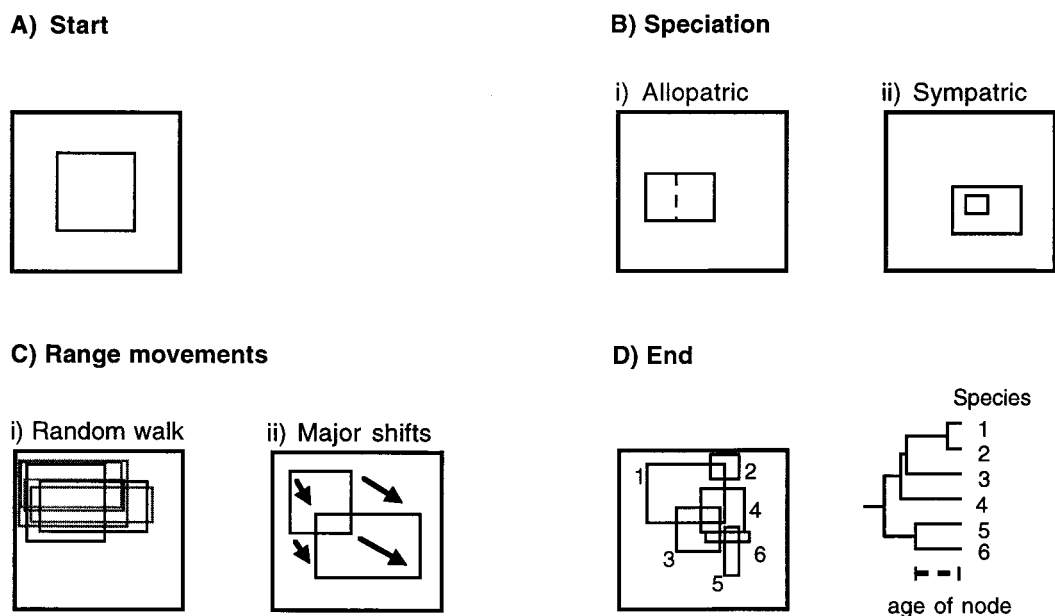


Figure 1: Simulation model for the evolution of species' ranges during cladogenesis. *A*, Model considers species with rectangular ranges occupying a square continental area. Diversification starts at time 0 with a single lineage. Lineages have a constant probability of splitting per unit time, leading to an exponential build-up of species numbers through time. *B*, At each speciation event, the ranges of descendent species are allocated according to the chosen mode of speciation. Allopatric speciation involves a dichotomous split at a uniform random point along either the horizontal or vertical edge of the species' range. Sympatric speciation involves the appearance of a new species within the range of an existing species (the maximum and minimum (x, y) coordinates of the new range are drawn from a uniform distribution of possible values). The frequency of these two modes is defined by the probability per speciation event that speciation is sympatric. *C*, Range movements are specified by random independent changes to the minimum and maximum (x, y) coordinates of each species' range. We consider two alternatives. First, we allow ranges to move by continuous random walk of their minimum and maximum (x, y) coordinates through time. The number of steps per unit time is drawn from a Poisson distribution so that small movements are more frequent than large ones. Step size is a small constant that can be scaled to vary the rate of movement. An example of the movement of a single range over time is shown (*C, i*). Second, we assume that species have a constant probability per unit time of undergoing a major shift to their ranges, upon which their minimum and maximum (x, y) coordinates are set to random points from a uniform distribution within the continental area (*C, ii*). The frequency of range shifts can be varied. The continent presents a boundary to range movements: parts of ranges that step outside the continent are truncated before the next iteration. For simplicity, we do not include extinction in this model. Instead, species are prevented from reaching 0 range size: if the maximum coordinate drops below the minimum coordinate within a time step, the maximum and minimum coordinates are simply switched to ensure positive range size. Hence, species close to 0 range size maintain small, but positive, range sizes until any such time that the maximum coordinate moves away from the minimum coordinate again. *D*, Endpoint of each simulation is a series of species' ranges and a phylogeny showing the sequence and timing of splits leading to those species.

(Barraclough et al. 1998). Sister species may tend to display low sympatry simply by chance placement of their ranges within a large continental area. For example, one possible formulation of this situation is to allocate the present-day range of each species in our simulation model as randomly chosen points within the continental area (i.e., the maximum and minimum $[x, y]$ coordinates are drawn from a uniform distribution of possible values). This model produces a roughly log-normal distribution of range sizes (see "Peripatry" below). Samples of sympatry versus node age plots under this model are shown in the third column of figure 3. The plots display little overlap between recently split species, apparently consistent with allopatric speciation, but in fact species' ranges provide no information

on the mode of speciation in this case. The mean intercept obtained over repeated trials is shown in figure 4.

The above predictions assume that species' ranges move at random and independently of one another. However, additional processes affecting species' ranges may also influence our ability to detect the mode of speciation. For example, if species compete for similar ecological resources, then allopatric distributions may be maintained by competitive exclusion (Letcher et al. 1994). In principle, this might obscure the pattern of speciation, most seriously if species formed in sympatry were subsequently forced into allopatry by competition. Although this cannot be ruled out, most if not all models of sympatric speciation require mechanisms permitting the coexistence of sym-

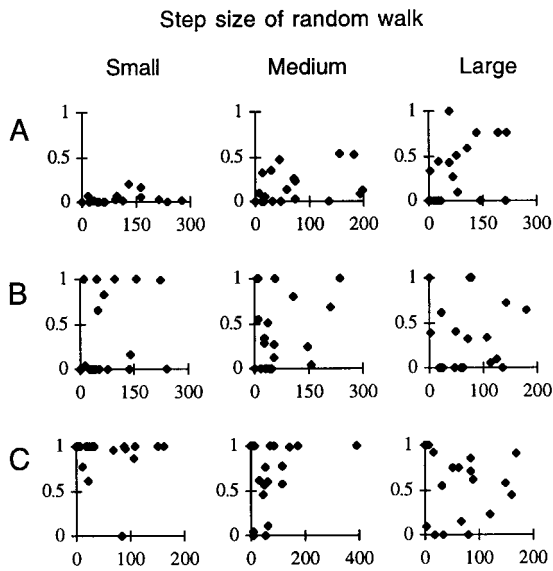


Figure 2: Samples of sympatry versus node age plots obtained when range movements occur by the random walk model. The frequency of allopatric and sympatric speciation varies among rows. A, Entirely allopatric. B, 50% sympatric. C, Entirely sympatric speciation. The Y-axis is the degree of sympatry, and the X-axis is the age of nodes in units time. Simulations started with an ancestral range of 200×200 units in a continental area of 220×220 units. The per-lineage probability of speciation was 0.01 per unit time. They were stopped once 20 species have evolved. The number of range steps occurring per unit time was drawn from a Poisson distribution with $\bar{X} = 0.1$; that is, steps occurred at 10 times the rate of speciation events. The overall level of range movement was then varied by scaling the step size from small (step size = 0.2 units), to medium (=2.0 units), to large (=20 units).

patrically originating forms, so subsequent competition seems unlikely. However, the sympatric origin of species could be obscured if competition were too weak to prevent the initial establishment of sympatric forms but strong enough to favor populations that escape from sympatry and if subsequent movement into allopatry occurred over shorter timescales than those elapsed since the most recent speciation events. It has been suggested to us by a referee that sympatric speciation by chromosomal rearrangements could fulfil these requirements. Information on chromosomal structure and ploidy levels could be used to test this possibility, but in the absence of additional evidence, we believe it remains an unlikely bias. For species originating by allopatric speciation, competitive interactions may delay the origin of sympatry until species have diverged in phenotype sufficiently that competition no longer occurs, thereby accentuating the pattern obtained under neutral range movements. The effects of competition and how we might detect them are discussed further below.

Real Examples

Plots from the sample groups are shown in figure 5. Correlation coefficients and intercepts are shown in table 1. Correlation coefficients were determined using Spearman's rank tests. So that the intercept of each plot could be estimated, regression lines were fitted following arcsine transformation of the degree of sympatry. Model criticism revealed that residuals from the lines were normally distributed but showed slight increase in variance at intermediate fitted values in a few groups. Nonetheless, the fit is good enough to provide a reasonable measure of the intercept.

The results can be summarized as follows. First, in all cases, intercepts are distributed around 0, and in most cases, the most recent nodes display 0 sympatry. There are two exceptions to the latter generalization: the fruitfly genus *Rhagoletis*, which has one very recent node with sympatry of 1.0 (between *Rhagoletis chionanthi* and *Rhagoletis osmanthi*), and the tiger beetle subgenus *Ellipsoptera*, which has one recent node with sympatry around 0.47. The genus *Rhagoletis* has provided the classic example of sympatric race formation by host shifts (Bush 1969). Note

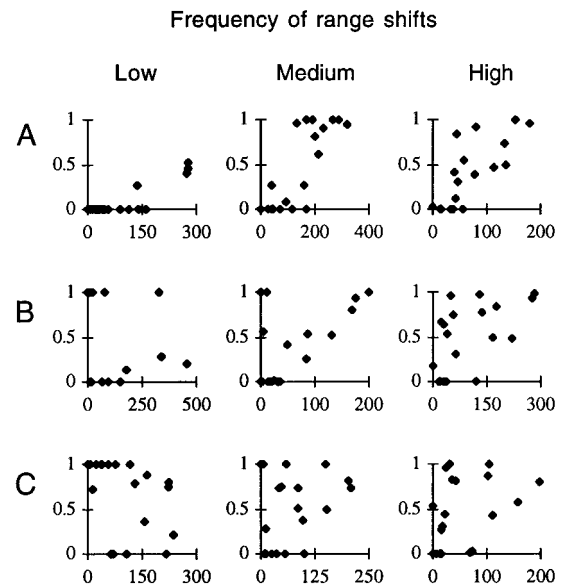


Figure 3: Sympatry versus node age plots obtained when range movements occur by large-scale shifts to entire species' ranges. The frequency of allopatric and sympatric speciation varies among rows. A, Entirely allopatric. B, 50% sympatric. C, Entirely sympatric speciation. The Y-axis is the degree of sympatry, and the X-axis is the age of nodes. The frequency of range shifts varies from low (=0.01 per unit time, the same rate as speciation), to medium (=0.05 per unit time), to high (the extreme case in which all species' ranges have shifted to random locations since the most recent speciation event). Other details are as described in figure 2.

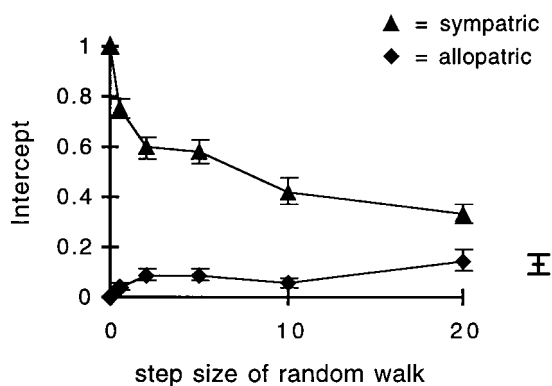


Figure 4: Effect of increasing range movements on the intercept of sympatry versus node age plots. Each point is the mean intercept from 15 trials of the random walk model outlined in figure 2. Standard errors are shown. Intercepts were fitted following arcsine transformation of sympatry, for reasons discussed in the text. Under higher levels of range movements, the intercepts obtained under entirely allopatric (*diamonds*) and entirely sympatric (*triangles*) speciation converge toward an intermediate value. A similar pattern is found using the range shift model (not shown). The bar to the right of the graph shows the mean intercept obtained when all species' ranges have shifted to random points within the continent; that is, ranges retain no information on the mode of speciation.

that two species within the group, *Rhagoletis zephyria* and *Rhagoletis mendax*, are embedded within the species *Rhagoletis pomonella* in the source phylogeny. Our method cannot address patterns within a paraphyletic clade of this kind because the exact sister groups of *R. zephyria* and *R. mendax* within *R. pomonella* are unknown (see appendix). *Rhagoletis mendax* is entirely overlapped by part of the range of *R. pomonella*, and so this may represent an additional recent split with high sympatry, whereas *R. zephyria* displays only slight overlap with other *R. pomonella* populations. However, despite one and possibly two recent sympatric splits, the pattern in the remainder of the group appears not to be suggestive of predominant sympatric speciation since other recent nodes display sympatries well below 1.0.

Second, in all groups, sympatry tends to increase with relative node age suggesting that range changes have occurred in these groups. There is variation in the pattern of this increase among groups, ranging from *Malurus*, the cranes, and *Xiphophorus*, with a majority of allopatric splits even between quite ancient splits, through to *Sylvia*, the auks, *Rhagoletis*, *Flexamia*, and *Ellipsoptera*, with a high degree of sympatry even among quite recent splits and a large scatter of values. The plots in the latter clades resemble closely those obtained under a null model of random ranges (third column, fig. 3). Hence, we cannot rule out the possibility that present ranges may have changed

so much that they provide unreliable information on modes of speciation.

In combination, the observation of low intercepts and increasing sympatry with relative node age suggests a general pattern of allopatric speciation with range changes leading to a build-up of sympatry over time. However, as outlined in the previous section, similar patterns may be obtained when there are large-scale range changes, irrespective of mode of speciation. Possible ways to determine whether current ranges retain information on mode of speciation will be discussed below.

Peripatry

Methods

Using the shaded range maps, we calculated the degree of range size symmetry at each node, defined as the range size of the clade with the smaller range divided by the sum of the range sizes of each clade:

$$\frac{\text{range of clade 1}}{\text{range of clade 1} + \text{range of clade 2}}$$

where clade 1 has the smaller range size. The measure takes values between limits of 0.0 and 0.5, the latter representing sister clades with equal-sized ranges. Lynch (1989) and Chesser and Zink (1994) used a similar measure in their assignments of peripheral-isolates speciation. We plot the degree of symmetry against relative node age.

Predictions and Simulations

We extend the approach outlined in the previous section to provide a statistical framework for testing the theory of peripatric speciation. Under a model of predominantly peripatric speciation, the geographic ranges of recently split sister species should tend to display asymmetry of range size. Under the alternative model that small population size, and hence range size, does not increase the likelihood of speciation, we expect no particular tendency toward range size asymmetry. One simple null model for this alternative is that, at speciation, the range of the ancestral species is split into two randomly sized fragments, in other words that a split occurs at some random point within the ancestor's range. This corresponds to a broken stick model, similar to those commonly used in other areas of evolutionary ecology (MacArthur 1960; Naeem and Hawkins 1994; Nee et al. 1996); hence, we refer to it as the "phylogenetic broken stick." It produces an even distribution of range size symmetry immediately after speciation that ranges from 0.0 to 0.5 with a mean value of 0.25. Lower values would suggest a tendency toward range

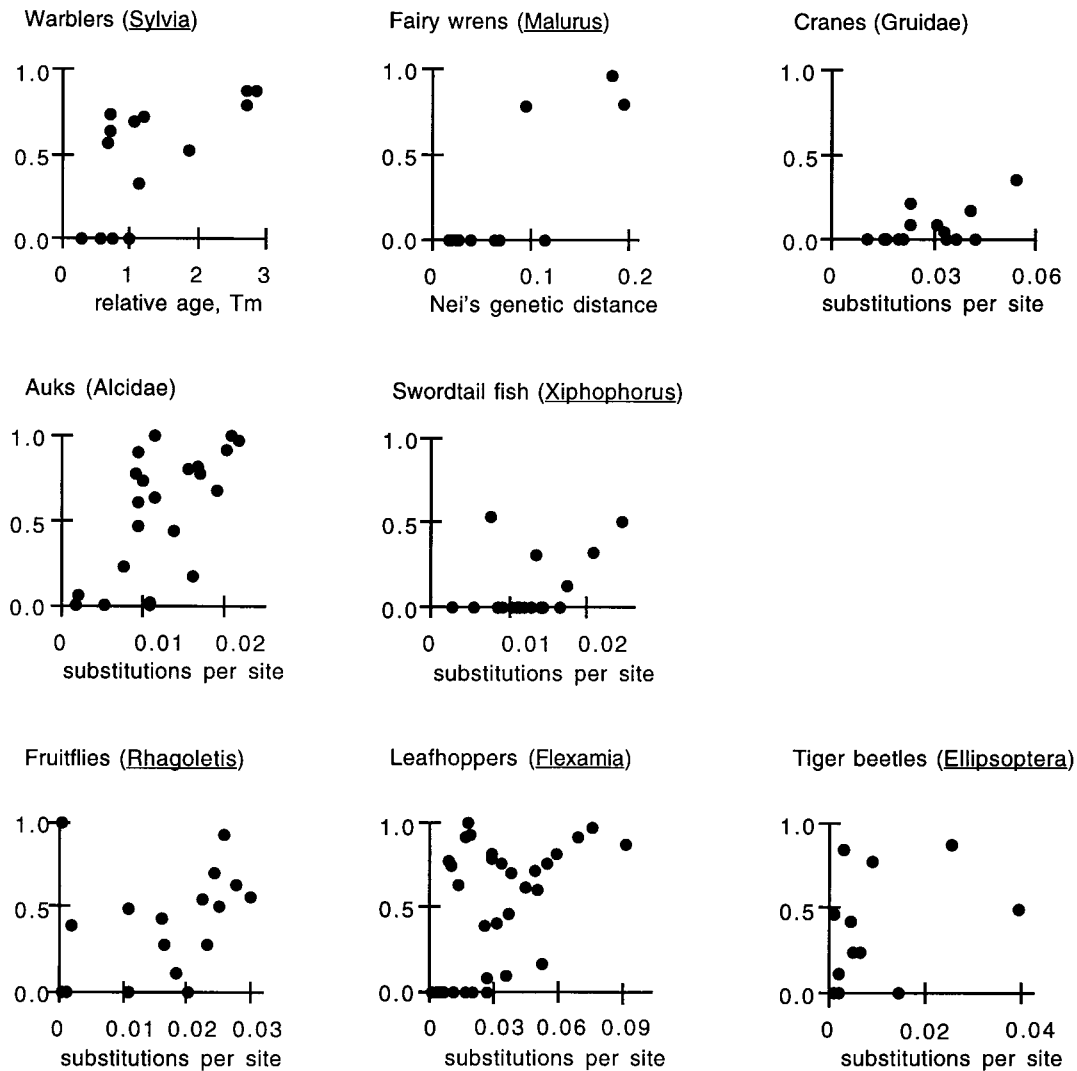


Figure 5: Plots of the degree of sympatry against relative node age in representative clades. The Y-axis is the degree of sympatry, and the X-axis is relative node age. Units vary among clades depending on the molecular markers used in the source phylogenies.

size asymmetry and the possible importance of small ranges in speciation. The degree of symmetry between older sister clades will depend on the nature of subsequent range changes. If range movements occur within a finite continental area, then older clades will tend to occupy a greater proportion of the total area and range size symmetry may increase with node age.

Figure 6 shows sample plots obtained using the simulation model outlined above. At low levels of range movement, the phylogenetic broken stick model produces the expected even distribution of symmetries. However, increasing the level of range movements increases the slope of plots and reduces the intercept slightly below 0.25 (fig. 7). For comparison, we show results from an arbitrary

asymmetric model in which ranges are allocated at speciation with a bias toward asymmetric ranges (details in legend of fig. 6). Our ability to distinguish the two modes of speciation declines as the level of range movements increases (fig. 7). Note that, because our measure of range size symmetry is bounded between 0.0 and 0.5, the value of range size symmetry was doubled and arcsine transformed before fitting intercepts to plots by linear regression (Sokal and Rohlf 1981).

As before, we also consider the expected pattern of symmetry when all species' ranges have shifted to random locations since the most recent speciation event. In this case, symmetry between sister species will depend on the statistical distribution of range sizes among species, since

Table 1: Summary statistics for plots of the degree of sympatry against relative node age

Taxon	<i>n</i>	Spearman's rank test		Intercept	Standard error of intercept
		r_s	<i>P</i>		
Warblers	14	.66	.02	.054	+.120 −.052
Fairy wrens	11	.76	.02	.049	+.091 −.045
Cranes	14	.54	.07	.012	+.046 −.012
Auks	22	.63	.004	.011	+.081 −.011
Swordtail fish	18	.47	.14	.024	+.082 −.024
Fruitflies	19	.48	.001	.174	+.185 −.127
Leafhoppers	35	.57	.06	.079	+.080 −.054
Tiger beetles	12	.39	.21	.208	+.147 −.116

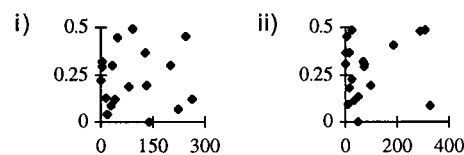
Note: Intercepts were fitted by linear regression of arcsine transformed sympatry, hence the standard errors of the untransformed intercept are asymmetric; *n* = number of nodes.

the ranges of sister species are effectively drawn at random from the available distribution. Although several forms of range size distribution can be imagined, we consider a single model in which range sizes are drawn from a simultaneous broken stick distribution; that is, we break a stick of given length at $n - 1$ uniform random points to produce n randomly sized pieces. Note that this model differs from the phylogenetic broken stick model where ranges were subdivided successively according to phylogeny. Our reasons for choosing the model are threefold. First, it corresponds to the range size distribution produced by the model of random range locations outlined in the “Allopatry or Sympatry” section. Second, it appears to match real distributions, leading to a left-skewed log normal distribution of range sizes similar to those commonly observed in real clades (Gaston 1998). Third, it allows straightforward simulation of expected patterns for real clades (see below) because the distribution of relative range sizes depends solely on the number of species within a clade. The pattern of symmetry across nodes will also depend on levels of range overlap, because the range size of higher clades depends on overlaps between their constituent species. A sample plot obtained under this model is shown in figure 6. In our simulations with 20 species the model produces an expected mean intercept of around 0.18 (fig. 7).

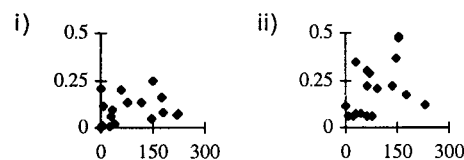
Real Examples

Plots of symmetry against relative node age are shown in figure 8. Intercepts are shown in table 2. They were fitted by linear regression of arcsine transformed values of symmetry, as described above. We used simulations to test for significant departures from the null expectations outlined above. First, we performed 1,000 simulations under the phylogenetic broken stick model, splitting an ancestral range successively according to the phylogeny for each group (assuming no subsequent range movements). From each simulation, we calculated the intercept of symmetry against node age to obtain the distribution of intercepts expected under this model. Second, we performed one 1,000 simulations allocating relative range sizes from a simultaneous broken stick distribution, corresponding to our model that species' ranges have shifted to random locations within a continental area. As noted above, the range size of higher clades depends in part on overlaps

A Phylogenetic broken stick



B Asymmetric model



C Simultaneous broken stick

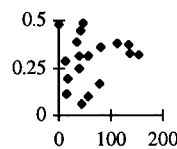


Figure 6: Samples of range size symmetry plots obtained under three models of range size allocation at speciation. *A*, Phylogenetic broken stick model, in which the ancestral range is subdivided at a uniform random point along its perimeter. *B*, Arbitrary asymmetric model, in which the probability of a split occurring increases in proportion to the square of its distance away from a 50 : 50 split. *C*, Simultaneous broken stick model in which the minimum and maximum (x, y) coordinates of each species' range are set to random points from a uniform distribution within the continental area. The *Y*-axis is the degree of symmetry, and the *X*-axis is the age of nodes. *A, B*, We show two levels of range movements: no range movements and a random walk model with a step size of 5.0 units. Other details are as described in figure 2.

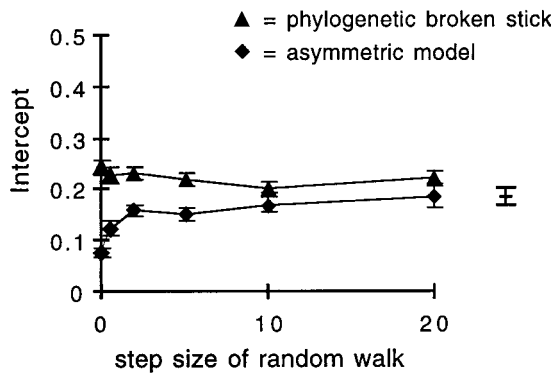


Figure 7: Effect of increasing range movements on the intercept of range size symmetry versus node age plots. Each point is the mean intercept from 15 trials using the random walk model. Standard errors are shown. Intercepts were fitted following doubling and arcsine transformation of range size symmetry, for reasons discussed in the text. Under high levels of range movements, the intercepts obtained under the arbitrary asymmetric model of range subdivision (*diamonds*) converge on those obtained under the phylogenetic broken stick model (*triangles*). A similar pattern is obtained using the range shift model (not shown). The bar to the right of the graph shows the mean intercept obtained in 15 trials of the simultaneous broken stick model of range allocation.

between their constituent species. Therefore, we used the observed overlaps for each node to calculate the range sizes of higher clades from the simulated range sizes of each species. Probabilities under the two models are shown in table 2. Correlation coefficients of the relationship between symmetry and node age were determined by Spearman's rank tests and are shown in table 2.

The results can be summarized as follows. Intercepts are lower than expected under the phylogenetic broken stick model in six groups. This difference is significant in the warblers, leafhoppers, and fruitflies, marginally non-significant in the fairy wrens ($P < .1$), and nonsignificant in the swordtail fish and tiger beetles. The intercept is higher than expected under the phylogenetic broken stick model in the cranes and the auks: only 5% of simulated trials produce a higher intercept in the latter group. When the eight groups are treated as independent tests, there is a significant deviation toward low intercepts across the study groups ($P < .001$, Fisher's combined probability; Sokal and Rohlf 1981). Similar probabilities are obtained under the simultaneous broken stick model. Although this is only one possible model for the distribution of range sizes following range shifts, it suggests that our results may be robust to the occurrence of random range movements. Symmetry increases with node age in the warblers, leafhoppers, and fruitflies (significant in the latter two groups) but decreases with node age in the remaining groups, most strongly in the auks ($P < .1$).

In conclusion, we find evidence for greater range size asymmetry between recently split sister clades than expected either by assuming random subdivision of ancestral ranges at speciation or under a simple null model for the random distributions of species' ranges within a continental area. The auks follow an opposite pattern with recent sister clades having more symmetric range sizes than older sister clades. Overall, the results appear consistent with a peripatric mode of speciation. However, alternative explanations will be discussed below.

Discussion and Conclusions

Our analyses utilize phylogenetic information and geographic ranges of present-day species to investigate the geographic pattern of speciation within clades. We use a simple model of cladogenesis and random range movements to help interpret observed patterns. Using this general approach, we looked at three issues.

Allopatric or Sympatric Speciation

We used the pattern of sympatry across nodes to estimate the general mode of speciation within each group, allopatric or sympatric. In nearly all cases, the most recent nodes are characterized by 0 range overlap between sister clades, suggesting a predominantly allopatric mode of speciation in these groups. This conclusion is unsurprising given the weight of evidence from other studies that sympatric speciation is likely to be relatively rare. However, the simulations show that similar patterns may arise if species' ranges are random with respect to cladogenetic history, simply because there is little chance of overlap between randomly placed ranges of sister species. For clades with large numbers of allopatric splits, such as *Malurus* and *Xiphophorus*, the observed low levels of overlap would seem unlikely to arise by chance placement of species' ranges. Hence, there appears to be positive evidence for allopatric speciation in these groups. However, plots for *Sylvia*, the auks, and *Flexamia* closely resemble those produced in simulations of the null model that species' ranges are distributed at random, suggesting that these plots may not provide reliable information on the mode of speciation.

In principle, we could test the null explanation by comparing the observed patterns of overlap to those obtained by randomly dropping species' ranges onto the continental area. However, formulating a realistic null model for a randomization of this kind is fraught with difficulties, including problems of defining the area available to the clade, treatment of the geometries of species' ranges and continents, and in choosing additional constraints to include in the model, for example, habitat restrictions (Strong et

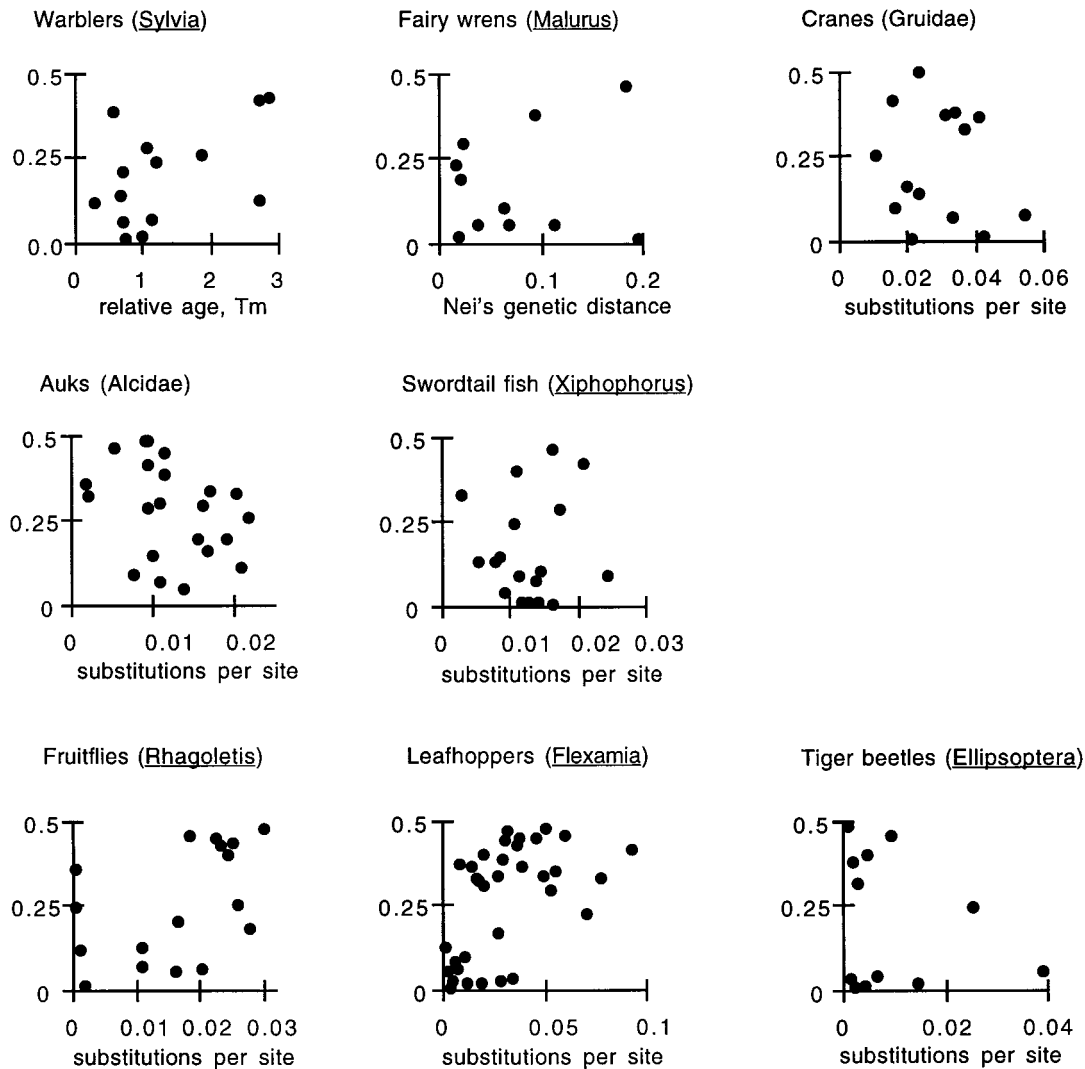


Figure 8: Plots of range size symmetry against relative node age in representative clades. The Y-axis is range size symmetry, and the X-axis is relative node age.

al. 1984; Gotelli and Graves 1996). On a case-specific basis, it may be possible to address these problems (Gotelli et al. 1997), but in the absence of such tests, we conclude simply that recent nodes tend to be allopatric in these groups. However, this may not reflect positive evidence of allopatric speciation in groups displaying rapid increases in sympatry with relative node age.

The recent sympatric splits observed in *Rhagoletis* and *Ellipsoptera* raise the possibility of a low incidence of sympatric speciation in those groups. In *Rhagoletis*, sympatric speciation seems plausible given the well-documented example of host shifts among races of *Rhagoletis pomonella* (Bush 1969, 1994). However, sympatry between recently split species may also arise through range changes occur-

ring after speciation. Our simulation results suggest that sympatric speciation may be detectable from biogeographic information alone only if it occurs at high frequencies, since then we observe a clump of recent splits distributed around 1.0, which is unlikely to arise through chance range movements alone (figs. 2, 3). Low levels of sympatric speciation will probably not be distinguishable from the effects of range changes. For both groups, the observed levels of sympatry between recent sister clades seem well within those obtainable under simulations of allopatric speciation with high rates of range change. However, we cannot rule out a low incidence of sympatric speciation as an alternative explanation.

An alternative approach to the problem of range changes

Table 2: Summary statistics for plots of range size symmetry against relative node age

Taxon	Spearman's rank test		Intercept	Phylogenetic broken stick (P)	Simultaneous broken stick (P)
	r_s	P			
Warblers	.39	.16	.08	.03	<.001
Fairy wrens	-.04	.91	.13	.07	.03
Cranes	-.16	.57	.3	.65	.56
Auks	-.36	.10	.4	.95	.98
Swordtail fish	-.09	.72	.14	.14	.30
Fruitflies	.50	.05	.12	.04	.04
Leafhoppers	.60	<.01	.12	.002	.006
Tiger beetles	-.11	.71	.22	.36	.44

Note: Sample sizes are the same as in table 1. Symmetry was doubled and arcsine transformed before fitting intercepts by linear regression. Probabilities of obtaining the observed intercept or less under the two null models are shown (calculations described in the text).

is to assess the likely extent of range changes during the history of the clade based on additional information (Chesser and Zink 1994). For example, paleoecological data regarding the effects of glacial cycles on the ranges of north temperate insect species (Elias 1992; Coope and Wilkins 1994) suggest that the insect groups we studied are likely to have undergone major changes since many of the speciation events represented on the phylogeny. Similarly, Blondel et al. (1996) discuss paleoecological evidence for likely range changes among species of *Sylvia* warbler. However, use of this method requires that nodes in the phylogeny are dated relative to the most recent known climatic events, which may prove difficult in some cases (Klicka and Zink 1997; Avise and Walker 1998). In addition, for many groups, fossil evidence on the likely extent of range movements is absent. Therefore, simulation analyses of expected patterns under different scenarios of range changes offer a useful additional tool for tackling this issue.

The Pattern of Sympatry within Clades

In addition to the mode of speciation, plots of the degree of sympatry versus relative node age provide information on the origin of sympatry in each group. In all cases, older sister clades tend to display greater levels of sympatry than younger sister clades. Irrespective of speciation mode, this pattern is only possible if species' ranges have changed since speciation events. Furthermore, it shows that sympatric species richness within these groups tends to be associated with range overlap between relatively distantly related species. This may occur as a result of random shifts in species' ranges over time, but alternatively there may be constraints to sympatry such that only species with accumulated ecological differences can coexist. By parti-

tioning sympatry among nodes, we may be able to distinguish these alternatives with further tests (Barraclough et al. 1998, 1999a). For example, in the *Ellipsoptera* tiger beetles, we find no evidence that levels of ecological divergence correlate with the degree of sympatry between sister clades (Barraclough et al. 1999b), thus failing to reject the possibility that sympatry arises through random range movements in this group. Similar tests may allow future evaluation of the role of competition in character divergence, and the build-up of sympatry, across a wider range of clades.

The pattern of increase in sympatry with node age varies among study groups. The fairy wrens, cranes, and swordtail fish display a pattern of predominantly vicariant distributions, with most nodes characterized by only low levels of overlap between sister clades. In contrast, the *Sylvia* warblers, auks, *Flexamia* leafhoppers, *Ellipsoptera* tiger beetles, and *Rhagoletis* fruitflies display much greater levels of sympatry with considerable range overlap between some even fairly recently split clades. Interestingly, the three insect groups display the highest levels of sympatry between recently split clades. Several possible factors may explain the differences among clades, including differences in their environmental histories, differences in dispersal abilities (Gutierrez and Menendez 1997; McCall et al. 1998), and/or differences in the strength of any interspecific interactions influencing geographic exclusion (Letcher et al. 1994; Brown et al. 1996; Gotelli et al. 1997). Our study groups compose an insufficient sample to look for correlates of sympatric versus vicariant distributions, but future comparisons among comprehensive samples of clades will allow tests for general correlates of sympatric species richness.

Peripatric Speciation

We used the pattern of range size symmetry across nodes to investigate the predictions of the peripatric model of speciation. Overall, we find that recently split sister clades display significant asymmetry in range size compared to two null models of range size allocation. The auks are an exception to this pattern, with greater symmetry between recently split sister clades than between older sister clades. The theory of peripatric speciation predicts that asymmetry arises because the genetic changes leading to new species are more likely to occur in small, narrowly distributed populations. However, there are at least two possible alternative explanations for the observed levels of asymmetry. First, in particular circumstances, asymmetry may result from the geometry of the landscape, for example, if a barrier promoting geographic isolation such as a mountain range happens to be located near the edge of a continental area (e.g., the Andes). Second, asymmetry may arise as a result of range changes occurring since speciation events. We considered one model of random range movements, but other types of movement may lead to higher levels of range size asymmetry between sister clades, for example, if major range contractions and/or expansions occur. Alternatively, some range movements may lead to greater symmetry between the ranges of sister clades, such as situations in which range size is heritable (Jablonski 1987; Ricklefs and Latham 1992). We cannot distinguish these alternatives here, but our approach provides a null model framework for future investigations of the predictions of the peripatric model and, more generally, of the geometry of species' ranges arising during cladogenesis.

Methodological Issues

Our approach requires a phylogeny and species' range data for all species within the study clade. Although species-level phylogenies of entire clades are relatively scarce at present, current levels of molecular automation mean they will soon be available for a wide range of representative clades, and they will be based on datasets of multiple markers. In addition to reconstructing the topology of cladogenetic splits, molecular phylogenies provide branch lengths that may be useful for estimating the relative ages of nodes. However, these estimates may sometimes incorporate substantial error because of rate variation among lineages and the intrinsic stochasticity of base substitutions (Mindell and Thacker 1996; Rambaut and Bromham 1998). Node level may be a useful surrogate measure for time since speciation in some situations but will be unreliable if nodes of equivalent level differ substantially in their ages. The reliability of branch lengths can be roughly

assessed by observing phylograms: if the tips roughly align, then branch lengths are likely to provide a reasonable estimate of relative ages.

Errors in estimates of species' ranges are likely to add noise to observed patterns. Although species' ranges may be undersampled in some groups, particularly rare or tropical ones, there is likely to be reasonable data for any group of sufficient interest to warrant a complete phylogenetic analysis. Information is typically presented in one of two forms: dot maps showing locality records or shaded distribution maps. The latter are usually calculated from the former, combined with the author's intuition of the entire range of each species. Shaded maps inevitably involve a simplification of the true distribution of species, but they provide a summary that allows calculation of areas and overlaps at the scale traditionally used for discussion of modes of speciation and factors influencing species' ranges. However, sympatry at the regional scale may not correspond to fine-scale co-occurrence. Interpretation of the implications of such sympatry, including mechanisms of sympatric speciation or levels of species interactions, should consider fine-scale species distributions as well.

Simulation of Species' Ranges

We introduced a simple model of cladogenesis, incorporating random movements of species' ranges, and used it to compare observed patterns of geographic range. Previous work has taken a related approach to island biogeography (Collwell and Winkler 1984; Hayden et al. 1993) and used similar models to investigate spatial patterns of genotypes within continuous populations (Neigel and Avise 1993). Our model differs in considering contiguous species' ranges occupying continental systems and in our express aim of generating broad predictions to guide phylogenetic analyses. The simulations use two specific models of range movements and rely on a rectangular geometry, but we believe our general conclusions are robust to other formulations of random changes to species' ranges. Future models could test this assertion and include additional features. For example, we have not considered the effects of extinction on observed patterns. Random extinction of species may add noise to observed patterns of sympatry and asymmetry by removing parts of the range of higher clades. However, this may not greatly reduce our ability to discriminate modes because random extinction may tend to prune relatively older branches from a phylogeny, leaving recent splits relatively unaffected (Nee et al. 1994). Nonrandom extinction of species with relatively small ranges may tend to reduce asymmetry between extant sister clades but would perhaps have less effect on patterns of sympatry. More sophisticated spatial models of cladogenesis may prove useful in investigating this and related

questions into the origin and movements of species' ranges.

In conclusion, our results show how phylogenetic analysis of species' range data can help illuminate the role of geography in speciation and the pattern of subsequent changes in species' ranges. We find a general pattern of increasing sympatry with relative node age across the groups examined. This is consistent with a predominantly allopatric mode of speciation, and with postspeciation range changes leading to increased sympatry among species. The alternative explanation, that sufficient changes in species' ranges have occurred to obscure the mode of speciation, may be equally consistent in some of the groups. We discussed ways to assess this problem. In addition, we find a general pattern of lower levels of range

size symmetry between recently split species than expected under two null models of range allocation. This may reflect intrinsic influences of population size on the probability of speciation, as predicted by the peripatric model of speciation. However, other factors may also lead to asymmetric ranges between sister clades. We believe that development of this approach will help to unravel the general processes behind the geographic pattern of species diversification.

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Appendix

Table A1: List of clades used as examples

Clade	Number of species sampled	Molecular marker	Source of phylogeny	Sources of range data	Distribution of group
Fairy wrens (genus: <i>Malurus</i>)	12/12	Allozyme	Christidis and Schodde 1997	Rowley and Russell 1997	Australia and New Guinea
Sylvid warblers (genus <i>Sylvia</i>) ^a	15/16	DNA-DNA	Blondel et al. 1996	Baker 1997	Palaearctic
Auks (family: Alcidae)	23/23	Sequence	Friesen et al. 1996	Gaston and Jones 1998	Holarctic
Cranes (family: Gruidae)	15/15	Sequence	Krajewski and Fetzner 1994	Johnsgard 1983	Worldwide
Swordtail fish (genus: <i>Xiphophorus</i>)	19/22	Sequence	Meyer et al. 1994	Rauchenberger et al. 1990; Rosen 1960, 1979	Central America
Fruitflies (genus: <i>Rhagoletis</i>) ^b	20/21	Sequence	Smith and Bush 1997	Foote et al. 1993	Nearctic
Leafhoppers (genus: <i>Flexamia</i>)	36/44	Sequence	Dietrich et al. 1997	Whitcomb and Hicks 1988	Nearctic
Tiger beetles (subgenus: <i>Ellipsoptera</i>)	13/13	Sequence	Barraclough et al. 1999b	Pearson et al. 1997	Nearctic

^a In the genus *Sylvia*, we consider the monophyletic group of 16 species identified by the source phylogeny, which does not include two species (*Sylvia atricapilla* and *Sylvia borin*) traditionally placed in the genus.

^b In the genus *Rhagoletis*, we consider the monophyletic group containing 21 North American species identified in the source phylogeny. One species, *Rhagoletis pomonella*, is paraphyletic with respect to *Rhagoletis mendax* and *Rhagoletis zephyria*. Since our methods compare monophyletic sister clades, we compare the clade *R. pomonella*, *R. mendax*, *R. zephyria* to its sister clade but cannot consider finer patterns within this group.

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